Plant population processes in the course of forest succession in abandoned meadows. II. Demography of succession promoters

KRYSTYNA FALIŃSKA*

Botanical Institute, Polish Academy of Science, Kraków Poland

(Received: October 17, 1988. Accepted: February 14, 1989)

Abstract

The studies on populations in the course of forest succession in abandoned meadows (15 ha) were conducted for 15 years (1974-1988). It was found that the population size of species which took part in the successional process either changed directionally, i.e. developmental phases of populations conformed to the succession stages, or fluctuated, when no direct relationship between both was determined. Three types of population dynamics were distinguished: 1) developmental cycle (increase, decrease and equilibrium in population size) lasted as long as forest comeback; 2) developmental cycle accompanied one successional phase; 3) species appeared in cycles, as a series of populations in the course of long-term succession. Following species groups were distinguished regarding their role in the vegetation transformation in unmown meadows: 1) long-term promoters, present throughout succession and affecting both, changes in meadow vegetation, and initiation of tall-herb and brushwood communities; 2) short-term promoters, present in the first successional phases, especially at the stage of transformation of meadow phytocoenoses; 3) stenoeccious promoters, confined to various depressions, periodically or permanently overlogged. All succession promoters were characterized by: high fecundity, ability to form polycormones and clones, strong and long-lived underground organs, modification of life-cycles, dual reproductive mode.

Key words: properties of succession promoters, population dynamics types, succession phases, population phases

* Reprint requests to: Geobotanical Station, Warsaw University, 17-230 Białowieża, Poland

INTRODUCTION

The diversity and variability of floristic compositions in the course of succession is considered a result of dynamic equilibrium between colonization, establishment and decline of species. The process of turnover of establishment of species under various ecological conditions is related to their life-strategies, especially to: growth and reproductive modes, longevity of underground organs etc. (Harper 1977, 1985, Grime 1979, Rabotnov 1985). Growth mode of an individual is important to the colonization and establishment in new sites, especially under extreme or pioneer conditions when generative reproduction is highly limited (Callaghan 1980, Harris and Davy 1986). Hence, polycormonal species play a crucial role in the colonization and occupying of free space (Falińska 1985, 1986a, b).

It becomes a common opinion that mechanisms of species turnover in the course of succession can be determined only through the studies on the population dynamics of species taking part in the process (Horn 1976, Connell and Slatyer 1977, Falińska 1985, 1986a, b, Begon et al. 1986).

However, in order to analyse the relations between population fates and directional changes in vegetation a number of methodical conditions have to be fulfilled. For instance, population development should be followed for many years, starting from the initial phase till the phase of dynamic equilibrium, or total/partial species decline (Falińska 1985). This is possible only when the species: 1) colonizes new area, 2) comes back to the site previously occupied, or at least, 3) its population size changes considerably under the influence of some agent, e.g. in fields and meadows abandoned by man.

It is not always possible to gather data on the life and death of individuals in the populations of long-living species, especially those with clonal growth, due to both technical obstacles and to the fact that such studies require long time and much labour. For example, the data necessary in the demographic analysis of some herbs had been collected for 30-40 (Tamm 1972a, b, Inghe and Tamm 1985), or at least 10 years (*Narcissus pseudonarcissus* — Barkham 1980a, b; *Iris pseudacorus* — Falińska 1986b).

The present studies aimed to determine the role of herb species in the transformation of vegetation in abandoned meadows. The special attention has been paid to those species that are present in the whole successional process, from meadow to forest, but with different proportions in consecutive phytocoenoses. It has been attempted to answer following questions: 1) which species initiate the changes in meadow communities and lead to the formation of tall-herb and brushwood phytocoenoses; 2) what are the relations between phases of population development and succession stages; whether the development cycle of species populations, present throughout succession, is as the time of forest comeback, or whether these species constitute a series of consecutive populations; 3) what individual properties determine the species role as a promotor.

METHODS

The studies were conducted in the Reski Uroczysko in Białowieża Forest. The description of the area under study and hierarchical system of study areas constructed in order to analyse phytocoenoses, populations and individuals are given in part I (Falińska 1989). The species selected so as to determine the role of plant populational processes in the succession differed, regarding their biology and morphological properties. These were: *Cirsium palustre*, *C. salisburgense*, *Filipendula ulmaria*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Caltha palustris*, *Myosotis scorpioides*, and *Iris pseudacorus*.

Spatial population structure of selected species and their neighbours was analysed in twenty four 200 m² study areas. Each season, for 15 years, the scheme of population distribution was done at the 1:100 scale (Fig. 1). At flowering and fruiting the shoots of chosen species were counted. The studies on the architecture, growth and development of individuals were conducted on six 25 m² plots, divided into 1 m² quadrats. The plots were located in six study areas, selected as the most representative for the course of the analysed succession.

Each season the scheme was done at the scale 1:10 which showed: the distribution of individuals of main phytocoenose components, the size and shape of their areas, while in polycormonal species also the type of shoot distribution within these areas (Fig. 2). Every season on each plot vegetative (vegets > fragments of polycormones formed due to their desintegration) and generative (seedlings) individuals were counted and labelled (Fig. 2). These data were used to assess the role of individuals of different origin in the population dynamics, and the relationship between the age structure of a population and its part in the succession.

RESULTS

SUCCESSION PROMOTORS

The species role in the initiation, transformation and stabilization of phytocoenoses in the succession varied. In the structure and dynamics of vegetation in abandoned meadows the important part was played by species which were long present with high proportions in the structure of consecutive phytocoenoses. Three species groups were distinguished considering the relation between the dynamics of their populations and vegetation dynamics.

1. The species with changes in population size conforming to the directional transformation of vegetation, hence a) the population size increased in the initial phase of succession, i.e. in the period of quantitative changes in the structure of meadow communities; b) population size was maximum in the optimal phase of succession, i.e. in the period of qualitative changes — the formation of new phytocoenoses; c) dynamic equilibrium of population size

Fig. 1. Observations in 200 m² study areas — the method enabling to follow the fate of individuals and population, the case of one selected species (Falińska 1985, completed)

Filipendula ulmaria:

⊙ – one year old individuals	☼ – senile parts
⊖ – shoots	--- – clones
⊕ – boundary of a polycormones	V – vegets
▨ – <i>Salix cinerea</i>	□ – <i>Lysimachia vulgaris</i>
▤ – <i>Alnus glutinosa</i>	▲ – <i>Lythrum salicaria</i>
▥ – <i>Carex acutiformis</i>	☼ – <i>Carex cespitosa</i>

Fig. 2. Basic plots applied to observe the fates of individuals of different origin against the changes in the vegetation of abandoned meadows. Vegets – individuals derived through polycormone desintegration

was attained in the terminal phase of succession, i.e. in the period of development of forest phytocoenoses (Fig. 3).

This group includes: *Filipendula ulmaria*, *Lysimachia vulgaris*, and *Lythrum salicaria*. They were present in the whole successional process, although their proportions changed in the consecutive phytocoenoses. These changes either affected the transformation of vegetation or initiated new phytocoenoses. Such species are described as long-term promotors. *Filipendula ulmaria* seems the most typical, and its population dynamics has been considered as demographic pattern for long-term promotors.

2. The species with increase, decrease and dynamic equilibrium of population size in one successional phase. They dominated shortly, especially in the initial phase of succession, whereas later they were represented by single individuals, or even absent (Fig. 4). This group comprises: *Cirsium palustre*, *C.*

Fig. 3. Variation in populations in the course of succession, a — changes in population spatial structure for 14 years (1975-1988) in (10×20 m) permanent study area; b — age structure, developmental phases: I — seedlings, II — juvenile, III — mature, IV — subsenile, and V — senile individuals; c — changes in the number of individuals (N), and shoots (n)

Fig. 4. a — Changes in the density and fruiting fractions of populations (shaded), observed on 64 plots (5×5 m) of the transect (320 m long) through successive phytocoenoses. b — Changes in the population density after plateau phase; second peak co-occurs with the period of willow brushwood formation

salisburgense, *Polygonum bistorta*, and *Potentilla palustris*. Such species are described as short-term promoters, *Cirsium palustre* being a demographic pattern.

3. The species with the fluctuating population size. Increase and decrease in the population size was not directly associated with the phytocoenose sequence. The species inhabited specific sites, various depressions and slopes, in meadow, brushwood and forest communities, e.g. *Myosotis scorpioides*, *Caltha palustris* and *Iris pseudacorus*. Population dynamics of these species was connected more with the living conditions, like changes of water level in local depressions, than with the phytocoenose sequence. They are described as stenoecious promoters.

Group 1. Long-term promoters. *Filipendula ulmaria* demographic pattern

Population dynamics. In mown meadows the size of *Filipendula ulmaria* population was small and stable. For instance during five years the number of individuals per 1 ha ranged from 32 to 36, while shoot number oscillated between 93 and 107. As meadows became unmown the population size rapidly increased, however the recruitment rate of individuals (N) and shoots (n) differed between fragments of the meadow abandoned at the same time (1974). The comparison of N and n values between two 200 m² areas, located within 1 ha of a meadow, indicates that the differences between them have been maintained for 14 years (Fig. 5).

Fig. 5. Changes in the number of *Filipendula ulmaria* individuals (N) and shoots (n) in 200 m² study areas: a — monospecific *F. ulmaria* aggregations, b — *Carex acutiformis* aggregations

The highest rate of increase was noted when *F. ulmaria* was the first among meadow species to colonize the area. Then the number of individuals (N) rose tenfold, while that of shoots (n) — 100 times for five years (Fig. 5a). However, when *Carex acutiformis* became second colonizer, then N increased only threefold, while n — ten times (Fig. 5b).

The mechanism of changes can be presented as follows. In the first period of development of *F. ulmaria* population an increase in the number of individuals was accompanied by a rise of the number of shoots in polycormones, followed by the partial, or total occupation of space ($3000-5000 \text{ n} \cdot 200 \text{ m}^{-2}$). This inhibited seedling development and increased mortality of juvenile (rosettes) and monocormonal (one-shooted) individuals. Then, in 7-9 years of population development, there was a first decrease in its size (Fig. 5). However, at the same time, some of the polycormones started to desintegrate, new vegetative individuals (vegets) were formed, and the population size grew. In the consecutive 2-3 seasons a number of vegets died which again resulted in the reduction of population size (12-14 years of population development, Fig. 5).

In sites with *Carex acutiformis* the population size of *F. ulmaria* increased twofold in the first two seasons of meadow abandonment, whereas a gradual decrease in its size started after 7 years (Fig. 5). In sedge aggregations *Filipendula* individuals did not form multishoot polycormones and rarely desintegrated. Here, vegetative reproduction was, therefore, less important than in the former case. In 14 years among 25 individuals there were only 7 vegets (28%), which originated through the division of three polycormones. On the other hand, when *F. ulmaria* was the only colonizer, then among 60 individuals as many as 38 (63%) were vegets.

Among six areas in the meadow abandoned in 1974 the first type of population growth was characteristic of two, while the second — of one. In other three areas the increment rate of population was considerably higher which resulted in the formation of monospecific *F. ulmaria* aggregations. Among 24 analysed areas in as many as 17 *F. ulmaria* formed aggregations in 6-9 years. Hence, the demographic analysis of the species was conducted on one plot (25 m^2) located in the aggregation occupying 2310 m^2 (55×42).

Density. During 14 years of population development shoot density considerably increased from 5 to 82 individuals per 1 m^2 , and from 45 to 1406 per 25 m^2 . This resulted mainly from the propagation of individuals in their multiyear cycle, only to a lesser extent — from an increase in the number of monocormones. Density of the latter was rather small, even in the peak, and ranged from 1 to 20 per 1 m^2 , whereas the density of polycormone shoots oscillated between 30 and 82 m^{-2} .

At the maximum shoot number only 128 (among $1406 \cdot 25 \text{ m}^{-2}$) were produced by monocormones, remaining belonged to 108 polycormones with 3-60 shoots per one individual. Polycormones with 6-22 shoots were most frequent (Fig. 6).

Filipendula ulmaria

Fig. 6. Changes in the population of *Filipendula ulmaria* in consecutive successional phases: I — meadow, II — tall-herb communities, III — willow brushwood, IV — forest; a — number of individuals (N) and shoots (n); b — number of juvenile (N_j) and mature (N_M) individuals, c — number of mature individuals of generative (N_G) and vegetative (N_V) origin, ($N_M = N_G + N_V$) and clone number (N_C); d — the proportions of monocormonal (one-shoot) and polycormonal (multishoot) individuals in a population (the numbers indicate variation range of the shoot number in polycormones); e — variation in the proportions of generative (n_g) versus vegetative (n_v) shoots in a population; f — variation in proportions of individuals of generative (N_G) versus vegetative (N_V) origin

Generative offspring (N_G) developed every season. The number of seedlings in the area of 10 m^2 , during 14 years of observations ranged from 11 to 160. In total, 680 seedlings appeared, among them only 49 (6.2%) survived to juvenile phase. Seedling survivorship varied between years, four cohorts survived in 20-36%, whereas five — merely in 0.8-5%. Four cohorts experienced 100% mortality (Fig. 7).

First vegets (N_V) appeared in the 6th year of population development, when polycormones started to desintegrate. In total, 95 vegets developed for the next 9 (1979-1987) years, among them 79 (83%) survived till 1987. They originated from 12 individuals and formed 12 clones (N_C) (Fig. 6).

Fecundity and reproduction. Continuous, even though variable between years, seedling recruitment (population reproduction Fig. 7), was secured by the high, changing with age, fecundity (seed production) of *F. ulmaria* individuals. 3-7 Year-old individuals produced most seeds. The increased seed number resulted from the higher number of fruiting shoots and from the bigger seed production by one individual. At this age individuals produced 5 to 36

Fig. 7. Number and survival of individuals of generative (genets) and vegetative (vegets) origin in various cohorts (1974-1987)

shoots with, on average, 425 ± 156 seeds per one shoot. The seed number per one shoot was highly variable and oscillated between 12 and 3200.

The number of fruiting shoots in polycormones, and seed production varied within the same age group regarding the developmental phase of a population. For instance, in the colonization phase single shoots produced,

on average, 844 ± 554 seeds, whereas in the phase of increasing population size — as much as 1983 ± 1256 seeds were produced per shoot, while the number of fruiting shoots amounted to 243-364 per 25 m². On the other hand, the seedling number seemed irrespective of the high individual fecundity. On average, 2 to 16 seedlings appeared in 1 m² quadrats.

The relatively high proportion of juvenile individuals in 14-years' cycle of population development was prominent (Fig. 6). At first their number varied between years from 15 to 62, after ten years it was doubled. This was the effect of the increasing number of offspring with inhibited development, i.e. rosettes which did not achieve flowering and fruiting phases. As a rule *F. ulmaria* individuals fruited and flowered in the second, or third season. However, the number of individuals still in the form of rosettes increased in years. The process was parallel to the period of intense polycormone growth and clone development (Fig. 6). Juvenile individuals of various age (1-5 years) constituted the generative offspring bank, which had a crucial role in population rejuvenation in the period when high-density aggregations were formed.

Long-term promotor exhibited following properties:

a. Ability to form polycormones (multishoot organisms (Fig. 8)).

Fig. 8. Changes in populations of long-term succession promotors. Changes in individual (N) and shoot (n) number for 14 years; proportions of individuals of generative (N_G) and vegetative (N_V) origin; proportions of monocormones (one-shoot) and polycormones (multishoot) in consecutive succession phases: I — meadow, II — tall-herb communities, III — willow brushwood, IV — forest

- b. Organism longevity attained through rejuvenation of the structure of old underground organs.
- c. Individual ability to "move" due to the growth of peripheral and dying of central parts; this prevented the resource depletion in the site permanently occupied by one individual, and, at the same time, favoured both individual turnover in the population and species turnover in the community.
- d. Capability of replacing or complementing generative with vegetative reproduction under adverse habitat conditions, or at the competition increasing with succession (Fig. 8).
- e. Modification of the population age and size structure (Figs. 9, 10).

Owing to these properties the species became dominants or subdominants in the consecutive successional communities. The populations of long-term promoters achieved their dynamic equilibrium twice: under the conditions of mown meadows (population size very stable) and in the flood-plain forest phytocoenoses (Fig. 3).

Fig. 9. Changes in the shoot size and population age structure of long-term promoters in the successional process (I-IV, as in Fig. 8)

Fig. 10. Differentiation of individual biomass of long-term promoters in the successional process:
a — tall-herb community, b — forest phytocoenose

Group 2. Short-term promoters. *Cirsium palustre* demographic pattern

Population dynamics. In mown meadows single *C. palustre* individuals were distributed at random. Mowing considerably limited their development, as it fell on the flowering stage. Hence, only some individuals formed fruits, however in the amount sufficient to ensure the presence of this species in the phytocoenose. In 1974 (last hay-harvest) 128 randomly located individuals and one big aggregation of 140, that occupied the area of 124 m², were found on 1 ha of mown meadows. In abandoned meadows both size, and degree of clumping of *C. palustre* population increased considerably. In five years already four big (88, 95, 101, 141 individuals respectively) and ten small (12-48 individuals) aggregations were found within 1 ha. Moreover, 138 dispersed individuals grew between these aggregations.

Changes in the size of *C. palustre* population varied between meadow parts. Three types of population dynamics were distinguished (Fig. 11):

1. In the meadow parts with *Filipendula ulmaria* as a dominant *Cirsium* population size increased and decreased rapidly.
2. In the meadow parts with *Carex acutiformis* aggregations *Cirsium* population size increased gradually or rapidly, then attained short plateau followed by a decrease, and second equilibrium at the small population size.

Fig. 11. Population dynamics of short-term (*Cirsium*) and stenoecious (*Myosotis*, *Caltha*) promoters of succession, in the presence and absence of competitive species (1-3, see text)

3. In mown meadows population size was big, and small aggregations were formed. When in badly mown meadow parts willow individuals appeared, *Cirsium* population size first fluctuated, next decreased, due to the elimination of individuals by willows. The former grew for some time on the peripheries of *Salix* aggregations and in their gaps.

Fecundity and reproduction. *C. palustre* is a facultative biennial. Individuals form a rosette in the first season and flowering shoot in the second. Under adverse living conditions rosettes can grow for 2-3 seasons and flowering is delayed. In unmown meadows increasing density of tall herbs rose the fraction of suppressed individuals from 25 to 78% (Fig. 12). More than a half of suppressed individuals never attained flowering phase. This can be explained by the fact that only individuals with their rosettes 25-30 cm in diameter can flower, whilst, the diameter of rosettes, of even several-year-old *Cirsium* individuals that grew among sedges and tall herbs rarely exceeded 20 cm on

Fig. 12. Changes in *Cirsium* populations in the course of succession: a — differentiation of rosette size in meadow and tall-herb communities; b — the fraction of fruiting individuals (shaded), c — shoot height versus rosette size

Fig. 13. *Cirsium palustre* individuals in the aggregation of *Salix*, *Filipendula* and *Carex*

average (Figs. 12, 13). The chance of *Cirsium* individuals to go through the whole life cycle became slight with the development of tall-herb and brush-wood communities. In these phytocoenoses they appeared only on the peripheries of *F. ulmaria* and *Salix cinerea* aggregations, or in *Carex cespitosa* tussocks (Fig. 14), which might continue till the forest comeback.

Fig. 14. Variation in density and distribution of *Cirsium* individuals in the rosette (plain circles) and fruiting (shaded circles) phases for 14 years, i.e. till the formation of willow brushwood (cf. Fig. 13)

The populations of short-term promoters went through following transformations in the course of successional process. For the first 3-6 years of unmown meadows their population size considerably increased, even several times, while their spatial structure changed from random to clumped. Small aggregations were formed (Fig. 14). Their frequency grew from 5-10% to 50-70%. In meadows abandoned for 6-7 years population size and frequency decreased. Then, for the next 2-3 years population density and individual distribution were close to those typical of mown meadows.

An increase in the density of tall herbs ongoing in the course of the succession affected populations of some species in the same way as mowing, i.e. a) prolonged their life-cycle, b) decreased the fraction of individuals attaining the fruiting phase, c) diminished the fecundity and reproduction.

These species played a short-term part in vegetation transformation because in the initial phase of forest succession in meadows, just after their abandonment, the fecundity of individuals in the population rapidly increased.

Moreover, in the sod of abandoned meadows many gaps were formed which became inhabited by species with high seed production (e.g. *Cirsium*). Their establishment in unmown meadow, under the conditions of increased competition and density of other species, resulted from their ability to grow in a rosette form. Individuals of such species, *Cirsium* especially, early in their life-cycle developed rosettes composed of a few leaves. Growing rosettes occupies bigger and bigger areas, covered and shaded plant layer near the ground very efficiently (Fig. 15), restricting the development of other species. However, with the course of the succession less and less rosettes produced fruiting shoots. Hence, when 2-4 year-old rosettes died they were replaced not by seedlings but by polycormonal colonizers. This way the decline of some populations commenced which lasted till the formation of tall-herb communities. Sometimes a slight increase in *Cirsium* population size took place when willow aggregations were formed (Fig. 4). Then on their peripheries single, but large *Cirsium* individuals appeared and grew till the forest comeback.

Fig. 15. Spatial structure of *Cirsium* populations in 10-year-old unmown meadows. Polycormones form large groups composed of large rosettes (plain circles) and a few fruiting shoots (shaded circles)

Group 3. Stenoecious promoters. Local demographic patterns

The species of the group are both the elements of rich meadows and form distinct aggregations in mucks. The populations differed in their dynamics. The former regressed in abandoned meadows, the latter fluctuated (Fig. 11).

If in mown meadows overlogged depressions were devoid of vegetation, then in abandoned meadows they were successively colonized by such species as: *Iris pseudacorus*, *Myosotis scorpioides*, *Caltha palustris* and *Carex vesicaria*.

Mosaic patches, or monospecific aggregations were formed, which totally covered the site (Figs. 16, 17). The populations that colonized mucks exhibited first rapid increase in population size, and next high-level plateau, like in the population of *Caltha palustris* No 2 in Figure 11.

Fig. 16. Population mosaic of species inhabiting in-meadow mucks

POPULATION DYNAMIC TYPES IN THE SUCCESSION (FIG. 18):

1. The cycle of population development terminates during one successional phase. It can be divided into period of rapid increase and decrease in population size, and short equilibrium. Such species are crucial to the formation of polydominant meadow and to the further transformations of meadow vegetation.

Fig. 17. Aggregations of two species formed in a meadow muck 8 years after the last hay-harvest

2. The cycle of population development, increase, decrease and equilibrium in size, goes on through the forest succession in abandoned meadows. As a rule, such populations are of the biggest size in the intermediate succession phase when tall-herb communities are formed. Then populations increase their

Fig. 18. Model of population dynamic types in the successional process: I-IV — succession phases, 1-3 — species types distinguished with respect to their role in the succession (see text)

size, even 100 times, species becoming dominants or subdominants. Such populations with directional changes of their size are important in the transformation of meadow communities and in the initiation of consecutive phytocoenoses.

3. Population size fluctuates, more rarely changes in cycles. Such dynamic type is characteristic of the populations present in stable meadow and forest communities, and throughout the whole successional process. They inhabit continuously or periodically overlogged mucks.

DISCUSSION

The life, reproduction and death of individuals, hence the population dynamics of plant species are affected by many biotic, abiotic and interpopulational agents (Harper 1977). However, often only one of them is crucial to the consecutive stages of individual developmental cycle (Grime 1979), and to consecutive phases of population development (Tamm 1972a, b, Inghe and Tamm 1985, Rabotnov 1985, Falińska 1985, 1986a, b). Such factors include: shading (Barkham 1980a, b), plant interference (Sarukhan and Harper 1973, Sharitz and McCormic 1972, Gross 1980, Turkington and Harper 1979a, b, c), compact vegetation cover (Grubb 1977, Gross and Werner 1982, Schenkeveld and Verkaar 1984), habitat patchiness (Connel and Slatyer 1977), sometimes also weather conditions especially in annuals (Wilkoń-Michalska 1976, 1985, Watkinson and Harper 1978).

The observations on the fate of *Filipendula ulmaria* population, conducted for 15 years, have showed that all these agents determine demographic processes of the species present in the long-term succession. However, they differ in the intensity and role between consecutive phases of population development.

Mowing limits both vegetative reproduction and emergence of new individuals, so when it is terminated this undoubtedly triggers an increase in the size of *F. ulmaria* population. In the first few years in abandoned meadows both the number of individuals (N) and shoots (n) rises rapidly, which results in the formation of large aggregations. *F. ulmaria* becomes a dominant, a rank maintained for many years (Wolf 1979, Regnell 1980, Falińska 1985).

Filipendula ulmaria rapidly colonizes meadows due to its specific properties as a polycormonal organism: logarithmic growth of the shoot number, individual areas increasing in size and rapidly covered, high biomass production, fecundity growing with age, dual reproductive mode, especially under unfavourable life conditions. Long-term observations on labelled individuals of polycormonal species indicate that some properties of plants with group or rhizome colonization strategy (Harper 1985) can be characteristic of consecu-

tive developmental phases of a single species. For instance, young individuals can produce numerous highly branched rhizomes, enabling them to penetrate the space between species of a floristically rich meadow and to eliminate them. On the other hand, older individuals tend to form compact structures, composed of up to a hundred shoots, growing in the close vicinity and connected with long-lived and strong rhizomes. Then, the population has a pronounced clumped spatial structure. This is not only polycormone architecture that changes with their age, but also fractions of generative and vegetative offsprings in favour of the latter. This considerably prolongs the life of some genets in spite of the worsening environmental conditions. Due to the high plasticity, variable size, biomass and fecundity of individuals, polycormonal species are present throughout the succession, despite increasing competition from, e.g. trees. The variation of individual properties in the successional process has been often encountered (e.g. Kershaw 1973, Knapp 1974, Fekete and Melkó 1981, Falińska 1986a, 1988a, b).

All age-dependent changes influence the demographic process to a large extent. For example, the decline of *F. ulmaria* population after, more or less, twenty years has been usually interpreted as the effect of competition from trees, especially willows. However, the detailed studies on *F. ulmaria* recession and willow (*S. cinerea*, *S. pentandra*) encroachment showed that this has to be preceded by the senescence and dying of the former. Only then, the free space is occupied by willows, which by shading and mechanical damage gradually delimitate remaining polycormones. No willows entered the sites occupied by young polycormones with compact structure.

It has been often discussed whether dying of modules and other parts of long-lived organisms results from their senescence, hence whether it is an irreversible process of the worsening of their life conditions (cf. Turner 1950, Hamilton 1966, Bell 1984, Watkinson and White 1985). The reproduction has been frequently associated with the age of organism and its modules (Rabotnov 1985, Sarukhan 1980, Charlesworth 1980, Callaghan and Emanuelsson 1985). A population rejuvenates due to the organism ability to regenerate senile structures resulting in the constant emergence of new structures with high reproductive potential. Moreover, migration of new modules outside the area occupied by the oldest parts of an organism contributes to the specific "movement" of individuals in space. The process prevents total resource depletion, caused by the long-term occupation of one site by a single individual. Parallel processes of senescence and rejuvenation, characteristic of long-lived species prevent the stagnancy in natural populations, and at the same time enable them to be permanently present in a site, e.g. in the course of long-term succession.

Many demographic works are focused on density, as one of the agents that govern demographic processes. For instance, the phenomenon of autregulation in plant population is often discussed on the grounds of density-

-dependent: size and habit of individuals, and their ability to attain reproductive phase (White and Harper 1970, Harper and White 1974, Silvertown 1987). Simple relationships between density, and reproduction and mortality have been mainly observed in annuals, e.g. *Spergula vernalis* (Symonides 1974), *Vulpia fasciculata* (Watkinson and Harper 1978) and *Floerkea proserpinacoides* (Smith 1983a, b, c). For perennials the results obtained are more equivocal. In a number of perennial herbs individuals during their life-cycle produce many rooted shoots, hence an increase and a decrease in density is closely associated with the changes in the age structure of a population. Low population density of polycormonal species in the colonization phase results from the development of monocormones randomly located in the meadow sod. High rate of shoot propagation leads to the formation of polycormones, which successively occupy the area. This, in turn, restricts the development of juvenile individuals and seedling emergence. The question arises whether this is caused by population density or by specific interactions between mature organisms and offspring.

The distances between individuals determine their inter-relations that change with age, because plant requirement for space changes with their life-cycle (Begon et al. 1986). The density effect is usually considered with respect to individual number in a given area, and not to the distance between them. Moreover, such studies have been frequently conducted on tiny areas (0.5-1.0 m²), which enclosed only small fragments of populations, diversified regarding density and individual distribution in space. The results of the studies conducted at the microscale are applied to the processes ongoing at the macroscale. Two examples, one for an annual, and another for a perennial, illustrate well such phenomenon. Three aggregations of *Impatiens noli-tangere*, 10 m² each, were selected, then divided into 1 m² quadrats. Among 30, so obtained areas, only 4 were over-densed (more than 400 individuals · m⁻²), and solely there the habit, size and fecundity of individuals changed (Falińska 1986a, b, 1988a, b). In similar studies on *F. ulmaria* population among 25 quadrats, 1 m² each, only three were over-densed (more than 60 shoots · m⁻²), where adverse density effects were observed. It is worth stressing that both studies concerned high-density aggregations. In *F. ulmaria* populations it is difficult to distinguish the density effects from those caused by polycormone senescence. For instance, most polycormones attain their senile age (e.g. a decrease in the number of generative shoots and regenerative buds) at the maximum population density. Then, almost a half of single rosettes (juvenile individuals) and those inside polycormones do not attain further developmental phases. The rosettes with their diameter less than 10 cm (minimum size) do not form flowering shoots. Similar trends have been observed in monocarpic plants, such as *Dipsacus fullonum* (*D. silvester*) (Werner 1975, Caswell and Werner 1978), *Daucus carota* (Holt 1972), *Geranium robertianum* (Falińska and Pirożnikow 1983).

The results of the studies on fates of succession promoters indicate that their architecture, and intensity of rejuvenation and senescence change with age. It has been showed that these properties are a biological mechanism of species turnover in the course of the succession. This explains high conformity between the age structure of a population, and both phases of its development and succession stages (Fig. 3).

REFERENCES

- Barkham J. P., 1980a. Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). I. Clonal growth, seed production, mortality and the effects of density. *J. Ecol.* 68: 607-633.
- Barkham J. P., 1980b. Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). II. Changes in number of shoots and flowers the effect of bulb depth on the growth and reproduction. *J. Ecol.* 68: 635-664.
- Begon M., Harper J. L., Townsend C. R., 1986. *Ecology: individuals, populations and communities*. Blackwell Sci. Publ. Ltd, Osney Mead, Oxford.
- Bell G., 1984. Evolutionary and nonevolutionary theories of senescence. *Amer. Nat.* 124: 600-603.
- Callaghan T. V., 1980. Age-related patterns of nutrient allocation in *Lycopodium annotinum* from Swedish Lapland. *Oikos* 35: 373-386.
- Callaghan T. V., Emanuelsson U., 1985. Population structure and processes of tundra plants and vegetation. In: *The population structure of vegetation*. J. White (ed.), Dr W. Junk Publ., Dordrecht. pp. 399-439.
- Cawell H., Werner P., 1978. Transient behaviour and life history analysis of teasel (*Dipsacus sylvestris* Huds.). *Ecology* 59: 53-66.
- Charlesworth B., 1980. *Evolution in age-structured populations*. Cambridge Univ. Press. Cambridge.
- Connel J. H., Slatyer R. O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Nat.* 111: 1119-1144.
- Falińska K., 1985. The demography of coenopopulations of forest herbs. In: *The population structure of vegetation*. J. White (ed.), Dr W. Junk Publ., Dordrecht-Boston-Lancaster. pp. 241-264.
- Falińska K., 1986a. Dynamics and structure of plant populations in forest ecosystems. In: *Vegetation dynamics in temperate lowland primeval forests*. J. B. Faliński (ed.) *Geobotany* 8: 307-346. Dr W. Junk Publ., Dordrecht-Boston-Lancaster.
- Falińska K., 1986b. Demography of *Iris pseudoacorus* L. populations in abandoned meadows. *Ekol. Pol.* 34: 583-613.
- Falińska K., 1988a. Individual, population, phytocoenose. PWN (in press).
- Falińska K., 1988b. Succession as the effect of demographic processes of plant. (in press).
- Falińska K., Pirożnikow E., 1983. Ecological structure of *Geranium robertianum* L. populations under natural conditions and in the garden. *Ekol. Pol.* 31: 93-121.
- Fekete G., Melkó E., 1981. Reproductive allocation in the stages of sandy succession. *Acta Bot. Acad. Sci. Hungar.* 27: 351-364.
- Grime J. P., 1979. *Plant strategies and vegetation processes*. John Wiley Sons, Chichester-New York-Brisbane-Toronto.
- Gross K. L., 1980. Colonization by *Verbascum thapsus* (Mullein) of an old-field in Michigan: experiments on the effects of vegetation. *J. Ecol.* 68: 919-927.

- Gross K. L., Werner P. A., 1982. Colonizing abilities of "biennial" plant species in relation to ground cover: implications for their distributions in a successional serie. *Ecology* 63: 921-931.
- Grubb P. J., 1977. The maintenance of species-richness in plant communities; the importance of the regeneration niche. *Biol. Rev. Cambridge Philosoph. Soc.* 52: 107-145.
- Hamilton W. D., 1966. The moulding of senescence by natural selection. *J. Theoret. Biol.* 12: 12-45.
- Harper J. L., 1977. Population biology of plants. Academic Press, London-New York-San Francisco.
- Harper J. L., 1985. Population biology and evolution of clonal organisms. Modules, branches and the capture of resources. In: Population biology and evolution of clonal organism. J. B. C. Jackson, L. W. Buss, R. E. Cook (eds.). Yale Univ. Press, New Haven-London.
- Harper J. L., White J., 1974. The demography of plants. *Ann. Rev. Ecol. System.* 5: 419-463.
- Harris D., Davy A. J., 1986. Regeneration potential of *Elymus farctus* from rhizome fragments and seed. *J. Ecol.* 74: 1057-1067.
- Holt B. R., 1972. Effect of arrival time on recruitment mortality, and reproduction in successional plant populations. *Ecology* 53: 668-673.
- Horn H. S., 1976. Succession. In: Theoretical ecology: principles and applications. R. M. May (ed.), Blackwell, London. pp. 187-204.
- Inghe O., Tamm C. O., 1985. Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943-1981. *Oikos* 45: 400-420.
- Kershaw K. A., 1973. Quantitative and dynamic plant ecology. 2nd ed. Edward Arnold, London.
- Knapp R. (ed.), 1974. Vegetation dynamics. Dr W. Junk Publ., The Hague.
- Rabotnov T. A., 1985. Dynamics of plant coenotic populations. In: The population structure of vegetation. J. White (ed.). Dr W. Junk Publ., Dordrecht-Boston-Lancaster. pp. 121-142.
- Regnell G., 1980. A numerical study of successions in an abandoned, damp calcareous meadow in S Sweden. In: Succession symposium on advances in vegetation science. E.v.d. Maarel (ed.). Nijmegen, The Netherlands, May 1979: 123-130. Dr W. Junk Publ., The Hague.
- Sarukhan J., 1980. Demographic problems in tropical systems. In: Demography and evolution in plant populations. O. T. Solbrig (ed.). Blackwell Sci. Publ., Oxford. pp. 161-188.
- Sarukhan J., Harper J. L., 1973. Studies of plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. I Population flux and survivorship. *J. Ecol.* 61: 675-715.
- Schenkeveld A. J. M., Vekaar H. J. P. A., 1984. On the ecology of short-lived forbs in chalk grasslands. Drukkerij Elinkwijk BV, Utrecht.
- Sharitz R. R., McCormick J. F., 1972. Population dynamics of two competing annual plant species. *Ecology* 54: 723-740.
- Silvertown J., 1987. Introduction to plant population ecology. Longman Sci. Technic., London-New York.
- Smith B. H., 1983a. Demography of *Floerkea proserpinacoides* a forest-floor annual. I. Density-dependent growth and mortality. *J. Ecol.* 71: 391-404.
- Smith B. H., 1983b. Demography of *Floerkea proserpinacoides* a forest-floor annual. II. Density-dependent reproduction. *J. Ecol.* 71: 405-412.
- Smith B. H., 1983c. Demography of *Floerkea proserpinacoides* a forest-floor annual. III. Dynamics of seed and seedling populations. *J. Ecol.* 71: 413-425.
- Symonides E., 1974. Populations of *Spergula vernalis* Willd. on dunes in the Toruń basin. *Ekol. Pol.* 22: 379-416.
- Tamm C. O., 1972. Survival and flowering of some perennial herbs. II. The behaviour of some orchids on permanent plots. *Oikos* 23: 23-28.

- Tamm C. O., 1972b. Survival and flowering of some perennial herbs. III. The behaviour of *Primula veris* on permanent plots. *Oikos* 23: 159-166.
- Turkington R., Harper J. L., 1979a. The growth distribution and neighbour relations of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *J. Ecol.* 67: 201-218.
- Turkington R., Harper J. L., 1979b. The growth distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. II. Inter- and intra-specific contact. *J. Ecol.* 67: 219-230.
- Turkington R., Harper J. L., 1979c. The growth distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. IV. Fine-scale biotic differentiation. *J. Ecol.* 67: 245-254.
- Turner C. I., 1950. The reproductive potential of a single clone of *Pelmatohydra oligactis*. *Biol. Bull.* 99: 285-299.
- Watkinson A. R., Harper J. L., 1978. The demography of a sand dune annual *Vulpia fasciculata*. I. The neutral regulation of populations. *J. Ecol.* 66: 15-33.
- Watkinson A. R., White J., 1985. Some life-history consequences of modular construction in plants. *Phil. Trans. R. Soc. London B.* 313: 31-51.
- Werner P. A., 1975. Prediction of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia* 20: 197-201.
- White J., Harper J. L., 1970. Correlated changes in plant size and number in plant populations. *J. Ecol.* 58: 467-483.
- Wilkoń-Michalska J., 1976. Struktura i dynamika populacji *Salicornia patula* Duval-Jouve. *Dissertations of Nicolaus Copernicus Univ., Toruń.*
- Wilkoń-Michalska J., 1985. Structure and dynamics of the inland populations of *Salicornia patula*. *Vegetatio* 61: 145-154.
- Wolf G., 1979. Veränderung der Vegetation und Abbau der organischen Substanz in aufgegebenen Wiesen des Westerwaldes. *Schr. Reiche Vegetationskunde* 13: 115.

Procesy populacyjne roślin w toku sukcesji na porzuconych łąkach. II. Demografia gatunków promotorów sukcesji

Streszczenie

Badania nad losami populacji w związku z przebiegiem sukcesji roślinności na porzuconych łąkach (15 ha) były prowadzone przez 15 lat (1974-1988). Wykazano, że gatunki uczestniczące w procesie sukcesji charakteryzują bądź kierunkowe zmiany liczebności, tj. duża zbieżność między fazami populacji i fazami sukcesji, bądź zmiany fluktuacyjne, gdy liczebność populacji nie wykazuje prostej zależności z kolejno następującymi zbiorowiskami. Wyodrębniono trzy typy dynamiki populacji: 1) cykl rozwojowy (wzrost, spadek, równowaga), który trwa tak długo jak powrót lasu na porzucone łąki; 2) cykl rozwojowy, który realizuje się w jednej z faz sukcesji; 3) następuje seria populacji, a gatunek ten pojawia się cyklicznie w długotrwałej sukcesji. Ze względu na rolę gatunków w procesie przemian roślinności porzuconych łąk wyróżniono następujące grupy gatunków: 1) długotrwałych promotorów, a więc te gatunki, które są obecne w całym toku sukcesji i przyczyniają się do przemian fitocenozy łąkowych oraz inicjacji fitocenozy ziołoroślowych i zaroślowych; 2) krótkotrwałych promotorów, tj. uczestniczących w pierwszym okresie sukcesji, zwłaszcza w fazie przebudowy fitocenozy łąkowych; 3) promotorów "w szczególnych miejscach" — są to gatunki, które zasiedlają i wypełniają różnego typu niecki z utrzymującą się stale lub okresowo wodą. Promotorów sukcesji wyróżniają następujące właściwości: duża płodność, możliwość tworzenia poliklonoń i klonów, silne i trwałe organa podziemne, modyfikacja cyklu rozwojowego, dwa typy reprodukcji.